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Experimental analysis of soft-tissue fossilization – opening the black box

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ABSTRACT

Taphonomic experiments provide important insights into fossils that preserve the remains of decay-prone soft tissues – tissues that are usually degraded and lost prior to fossilization. These fossils are among the most scientifically valuable evidence of ancient life on Earth, giving us a view into the past that is much less biased and incomplete than the picture provided by skeletal remains alone. Although the value of taphonomic experiments is beyond doubt, a lack of clarity regarding their purpose and limitations, and ambiguity in the use of terminology, are hampering progress. Here we distinguish between processes that promote information retention and those that promote information loss in order to clarify the distinction between fossilization and preservation. Recognising distinct processes of decay, mineralization and maturation, the sequence in which they act, and the potential for interactions, has important consequences for analysis of fossils, and for the design of taphonomic experiments. The purpose of well-designed taphonomic experiments is generally to understand decay, maturation, and preservation individually, thus limiting the number of variables involved. Much work remains to be done, but these methodologically reductionist foundations will allow researchers to build towards more complex taphonomic experiments and a more holistic understanding and analysis of the interactions between decay, maturation and preservation in the fossilization of non-biomineralized remains. Our focus must remain on the key issue of understanding what exceptionally preserved fossils reveal about the history of biodiversity and evolution, rather than on debating the scope and value of an experimental approach.

Arguably the most scientifically valuable evidence of ancient life on Earth comes from fossils preserving remains of the decay-prone soft tissues (e.g. integument and muscle) that are usually degraded and lost prior to fossilization. These examples of 'exceptional preservation' and the fossil biotas from which they are recovered represent invaluable fossil archives, giving us a view into the past that is much less biased and incomplete than the partial picture provided by skeletal remains alone. Recent technological and methodological advances have allowed the acquisition of progressively more detailed anatomical and chemical data on fossil soft tissues and, as a result, reports of high fidelity preservation of anatomy (at micro- and macro- scales) and biomolecules are expanding the known limits of morphological and chemical fossil preservation. One component of current advances in the field is a reinvigoration of experimental investigations into the taphonomy of non-biomineralized organisms and tissues: laboratory-based analyses of post-mortem decay, maturation and mineralization, and the implications for processes of fossilization of soft tissue remains and biomolecules (e.g. Raff *et al.* 2008; Sansom *et al.* 2010; Sansom *et al.* 2011; Cunningham *et al.* 2012a; Cunningham *et al.* 2012b; McNamara *et al.* 2013; Murdock *et al.* 2014; Colleary *et al.* 2015; Naimark *et al.* 2016). This type of taphonomic experiment, focused on non-biomineralized remains, is the subject of this contribution; throughout, all references to 'taphonomic experiments' do not include those designed to address questions of skeletal taphonomy. We use the terms 'soft tissues' and 'non-biomineralized tissues' interchangeably, and to include sclerotized tissues.

The application of experimental taphonomy to exceptional preservation has developed over several decades (see Briggs and McMahon 2016 for a recent review), and has made major contributions to our understanding of how non-biomineralized tissues become fossilized. Experiments have provided significant insights, for example, into preservation of soft tissues through maturation and stabilization of organic compounds (e.g. Gupta *et al.* 2006; Gupta *et al.* 2009), processes of microbially mediated authigenic mineralization (e.g. Sagemann *et al.* 1999), microbial pseudomorphing of soft tissues (e.g. Raff *et al.* 2008; Raff *et al.* 2013), and how non-random patterns of anatomical decay can introduce systematic biases into the interpretation of exceptionally preserved fossils (e.g. Sansom *et al.* 2010; Murdock *et al.* 2014).

The value of experimental and analytical approaches applied to the study of exceptionally preserved fossils is beyond doubt, but we identify two issues that are hampering further progress. First, a lack of clarity regarding the purpose and limits of experimental approaches, and second, ambiguity in the use of terminology. More precise use of language and greater clarity regarding the rationale for conducting taphonomic experiments will allow researchers to focus on the key issue of what exceptionally preserved fossils reveal about the history of biodiversity and evolution, rather than the scope and value of an experimental approach.

DECAY, MATURATION, PRESERVATION AND FOSSILIZATION

Clarity regarding 'fossilization' and 'preservation' are clearly crucial to taphonomic analysis, otherwise we risk confusing processes with results, yet the terms are used interchangeably by some authors and to mean distinct and different things by others.

Fossilization is one outcome of the range of processes that affect an organism after death (Figure 1). These processes cumulatively result in both loss and retention of information, and can balance out in different ways, with the most obvious alternative outcome to fossilization being non-fossilization - the loss of features or complete absence from the fossil record. Every part of every organism ends up somewhere on a spectrum from partial to complete non-fossilization. We focus here on decay, maturation and mineralization as distinct processes resulting in information retention (preservation) and information loss.

Decay is the post-mortem process by which original biomolecules, tissues and structures are degraded and lost through abiotic processes (such as chemical thermodynamics) and biotic processes, such as autolysis and microbially mediated decomposition. For many researchers, the antithesis of decay is preservation, but preservation is not the same thing as fossilization (see below).

Preservation refers to the processes that directly result in retention of information (Figure 1); processes by which inorganic and/or organic chemical activity replicates the form or converts the remains of non-biomineralized tissues into minerals (mineralization) and organic compounds that

are stable over geological timescales (maturation). This conversion can be via replacement or replication by minerals (mineralization), chemical transformation through maturation of organic compounds, or a combination. Different types of preservation may occur at different stages of decay and maturation. This definition of preservation is neither new nor out of step with its widespread use in the taphonomic literature; it serves merely to clarify the distinction between preservation and fossilization.

Mineralization is replacement or replication of non-biomineralized tissues by minerals. It can occur at any stage post-mortem, pre- or post-burial, early or late, and different modes of mineralization can act at different times (and under different conditions) in the taphonomic history of a fossil. Different modes of mineralization can occur in different parts within the same carcass, linked to differences in microenvironments (McNamara *et al.* 2009). Although many exceptionally preserved fossils have been mineralized, mineralization is not a requirement for exceptional fossilization.

Maturation of organic remains occurs post-mortem, mostly post-burial, primarily in the diagenetic realm, and can involve processes resulting in degradation and loss of biological information and/or processes resulting in stabilization of organic compounds such that they can survive over geological timescales. Maturation thus includes elements of both loss and retention of information, with preservation of organic remains through maturation involving in situ polymerization of more labile compounds (e.g. Gupta *et al.* 2006; Gupta *et al.* 2009; McNamara *et al.* 2016).

Secondary transformations might be considered as an additional stage in the post-mortem history of a fossil. Like maturation, they can involve either loss or retention of information. Mineral replacements from early stages of preservation can be lost or altered by subsequent chemical activity under different conditions of diagenesis (iron sulfides converted to iron oxides, for example). And organic remains stabilized through low temperature polymerization might be oxidized, depolymerized or otherwise mobilized and lost during later, higher grades of maturation. Information loss through weathering will also be a factor, but we do not consider this further here.

Focussing on these processes of decay, mineralization and maturation clarifies the distinction between fossilization and preservation: fossilization of an organism's remains is one outcome of the balance and interactions between processes of information loss (decay and maturation) and preservation (information retention via maturation and mineralization). This balance can be expressed as two very simple equations:

1. processes of information loss > processes of information retention = no fossil
2. processes of information loss < processes of information retention = fossil

The balance and outcome reflected in equation 1 are far more prevalent than those of equation 2.

Original biological tissues, or components thereof, are either lost or transformed into materials that are stable over geological timescales, and the existence of a fossil, even the most exquisitely preserved, does not imply survival of its biological information without alteration and loss. In these terms, 'exceptional preservation' is shorthand for *part of the process* that results in exceptional fossilization; we should not ignore the unexceptional aspects of information loss.

THE RATIONALE FOR CONDUCTING TAPHONOMIC EXPERIMENTS

The goal of the vast majority of taphonomic experimental analyses is not 'experimental fossilization': their aim is not to *replicate* the fossilization process in the laboratory or field. This is because fossilization involves many variables, including both known and unknown unknowns, and multiple confounding variables mean that - if our focus is on understanding the processes of fossilization - the results of such fossil replication experiments, whether in general or for specific Lagerstätten, are unlikely to tell us much of interest. While their success could be evaluated in terms of whether they produce something that might look more or less like a fossil, the experiments can reveal little if anything about the various processes involved in fossilization. This is not to say that observations of what happens when organisms decay under natural conditions have no place: these observations can provide useful constraints on the design of taphonomic experiments, or guidance on what a fossil jellyfish might look like, for example. But crude experiments that attempt to replicate fossilization without controlling variables are, in effect,

treating fossilization as a Black Box (Figure 2). To understand the processes that control information loss and information retention, the processes which ultimately produce the outcome of fossilization, we need to see inside the box.

This is the focus of robust taphonomic experiments: experimental decay, experimental maturation, and experimental preservation. The purpose of well-designed taphonomic experiments is generally to understand these processes individually (thus limiting the number of variables involved and making experiments tractable). In particular, robust taphonomic experiments investigate how specific variables, e.g. environmental pH, availability of ions, diffusion rate, burial temperature, etc., have potentially affected the loss and retention of anatomical information and biased exceptionally preserved biotas.

A simplifying initial assumption of this reductionist approach is that there are no direct causal links between processes of decay, maturation and preservation. However, it is important to note that this assumption applies only to the *design* of taphonomic experiments and does not preclude finding evidence of links between the various processes of decay, preservation and maturation, either in fossil data or in experimental results (a good example being taphonomic experiments demonstrating that certain forms of mineralization require decay to establish the geochemical gradients across which they operate (Sagemann *et al.* 1999)). In general, analysing and understanding each of these processes is a prerequisite for clear understanding of potential interactions between them.

Recognising the distinction between processes, the sequence in which they act (Figure 1), and the potential for interactions, has important consequences for analysis of fossils; missing this point has led to some unjustified criticism of experimental approaches. There is no reason to assume, for example, that sequences of decay should provide a guide to sequences of preservation: decay commences first (Figure 1) and provides a timeline and pattern of morphological modification and loss — the products of decay, in the form of incomplete carcasses and decay-modified characters, are the substrate upon which the processes of maturation and mineralization act. It is the timing and interplay between processes of loss and retention that govern what anatomical structures,

tissues and biomolecules are ultimately fossilized, and this can be unravelled only if we understand the taphonomic patterns resulting from decay. Similarly, claims that decay experiments are not applicable to the fossil record because either the environment or the experimental taxon used is not a good analogue for what occurred in deep time are missing the point of controlled taphonomic experiments. The same is true of criticisms that taphonomic experimental models are not informative because fossilization in each deposit, taxon and even specimen reflects a suite of unique conditions. Were these criticisms to be levelled at experiments designed to transform carcasses into fossils, we would agree, but they carry little weight as arguments against the validity of taphonomic experiments as an approach to modelling the general parameters that control decay, maturation and mineralization and their respective roles in fossilization across environments and taxa.

TAPHONOMIC EXPERIMENTS AND COMPARATIVE ANATOMY OF EXCEPTIONALLY PRESERVED FOSSILS

It is important to point out here that taphonomic experiments can be designed to address a range of different questions. For some, the goal is to understand the environmental conditions in which organisms decayed and were ultimately preserved (e.g. Plotnick 1986; Kidwell and Baumiller 1990; Hellawell and Orr 2012), or the degree to which a fossil biota is diminished in diversity by the loss of soft bodied organisms. In such cases taphonomic signatures are a proxy for palaeoenvironment or for faunal completeness, and the loss of anatomical information translates into gains in geological data.

For much recent work, however, the purpose of taphonomic experiments is to provide better data upon which to base interpretations of the anatomy of fossil organisms and, in turn, more accurate reconstructions of phylogenetic relationships and evolutionary patterns. These endeavours rely on comparative anatomical analysis, and when applied to exceptionally preserved non-biomineralized fossils, this analysis is predicated on the assumption that differences between taxa are not simply the result of random taphonomic processes. This is a crucial point that is often overlooked, particularly in the most fundamental elements of comparative anatomy: the individuation of body

parts and characters, and determination of the suite of characters present in a taxon (see Rieppel and Kearney 2002 for discussion of individuation). Comparative analysis is possible only if the similarities and differences in characters reflect original anatomy and, critically, if taphonomic factors can be detected and taken into account. Furthermore, because comparative analysis ultimately requires comparison with extant organisms, investigators must distinguish differences that arise because of evolutionary history from those that simply reflect the incompleteness of the fossil (Donoghue and Purnell 2009). This decision can be based either on intuitions and assumptions, or on the crucial evidence generated by taphonomic experiments. We advocate the latter approach.

TAPHONOMY, EXCEPTIONAL PRESERVATION, AND EXPERIMENTS - A WAY FORWARD

The processes of decay, maturation, and mineralization are controlled by diverse factors that vary both spatially and temporally in how they act. A focus of future studies must be on deconvolving the relative impact of these processes on our reading of the fossil record of exceptionally preserved organisms and particular Lagerstätten. In many exceptionally preserved fossils, the suite of characters present does not correspond to what might be predicted from a simplistic application of experimental decay results (i.e. the fossils are not simply a collection of the most decay resistant body parts). This is because the effects of preservational processes, sometimes highly selective with regard to tissue types, are superimposed upon the results of decay; it is false reasoning to suggest that fossilization of more than just decay resistant remains in itself indicates that patterns and sequences of character transformation and loss observed in experimental decay deviate from those that occurred in particular fossils. To use a specific example, invertebrate nervous tissues decay rapidly under controlled experimental conditions (e.g. Murdock *et al.* 2014, Sansom *et al*. 2015), yet mounting evidence supports the interpretation that some exceptionally preserved biotas include specimens with fossilized nervous tissues (e.g. Ma *et al.* 2012; Strausfeld *et al.* 2016). There is no conflict here: the fossils do not falsify the experiments, and the experiments do not falsify the anatomical interpretations of the fossils. Together they highlight a gap in our understanding of how nervous tissues become fossilized (Murdock *et al*. 2014). We argue that decay experiments are the best starting point for understanding the biases and filters of

fossilization because it is upon decayed remains that the processes of maturation and preservation must operate.

Further work is also required to better understand the processes of mineralization and authigenic mineral replication of original tissue. Despite experimental studies of the processes of replication of soft tissues in calcium phosphate (Briggs and Kear 1993a, b; Briggs and Wilby 1996) and in pyrite (Grimes *et al.* 2001; Grimes *et al.* 2002) other authigenic minerals have received little attention (but see Martin *et al.* 2004; McCoy *et al.* 2015). Soft tissues may be preserved via multiple pathways in a single fossil (e.g. Butterfield 2002; McNamara *et al.* 2009) but the controlling factors have yet to be elucidated experimentally. Future studies focussing on these preservational processes will be especially critical for attempts to extract tissue-specific and taxonomic signatures from fossil specimens that preserve different tissues in different minerals. Similarly, greater understanding of how microbial communities are mediating both decay and mineralization is likely to yield significant new insights into preservational biases.

We have attempted here to clarify the essential elements and the terminology that form the conceptual framework of taphonomic experiments, and the value of considering decay, maturation, mineralization, and preservation as distinct but interacting processes. Greater emphasis on the rationale for conducting particular experiments will enhance experimental design, allowing taphonomists to construct more tightly constrained models of taphonomic processes. This reductionist approach allows us to see beyond the Black Box view of fossilization, and from these foundations we can build towards a more holistic understanding of the roles of — and interactions between — decay, maturation and preservation in the fossilization of non-biomineralized remains.

Contributor statement. MAP, SEG and DJEM outlined the framework for discussions, and these concepts were subsequently developed by all the authors. MAP produced the initial draft of the manuscript; all authors contributed to its subsequent development and are listed alphabetically.

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A

FOSSILIZATION			
	INFORMATION LOSS		INFORMATION RETENTION = PRESERVATION
	DECAY	MATURATION	MINERALIZATION
PROCESS	Processes occurring post mortem, pre- or post-burial, resulting in degradation and loss of biomolecules, tissues and anatomical features	Processes occuring post-mortem, and mostly postburial, in pre-diagenetic, diagenetic and low temperature/pressure metamorphic realms, resulting in loss of biomolecules, tissues and anatomical features	Processes occuring post-mortem, and mostly postburial, in pre-diagenetic, diagenetic and low temperature/pressure metamorphic realms, resulting in transformation of biomolecules, tissues and anatomical features (including products of decay and maturation) into organic compounds that are stable over geological timescales	Processes occurring post mortem, pre- or post-burial (in pre-diagenetic and diagenetic realms) resulting in replication or templating of tissues and anatomical features by minerals that are stable over geological timescales
EFFECTS	• Decomposition • Autolysis • Microbially mediated decay • Loss of structural integrity • Disarticulation • Collapse • Physical distortion	• Abiotic oxidation, depolymerization and mobilization of biomolecules and products of decay and maturation • Physical compaction	• Polymerization of biomolecules and breakdown products formed during decay	• Authigenic mineralization and templating of soft tissues • External molding of features by early diagenetic mineralization

B

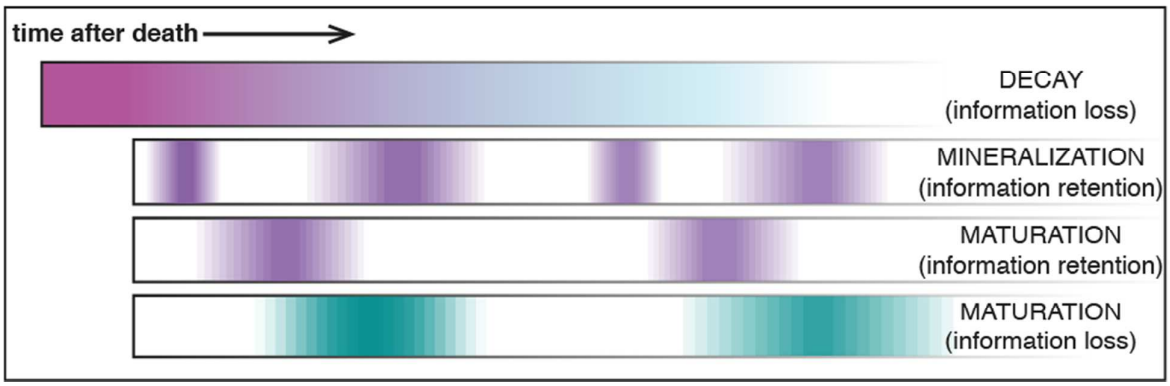

Figure 1. A. Terminology for processes involved in fossilization. B. The sequence of action, effects and potential timespan over which processes act. Processes are not continuous; intervals when processes (horizontal bars) are operating more intensely are shown by more intense colours; the relative timing and duration of periods of more intense loss and retention of information (via mineralization and maturation) are schematic. Decay starts before other processes but the potential timespan over which it operates is shorter. It is irreversible, and the rate of decay is not constant. Mineralization can start before maturation, but not before decay has commenced, and can occur at any subsequent point, although not continuously (multiple phases of mineralization are possible). Mineralization that post-dates decay can only preserve information previously retained through either mineralization or maturation. Maturation, both information loss and retention, can start before or after mineralization and can occur at any subsequent point. That maturation is a process that promotes both information loss and information retention does not imply separation of these processes in fossilization. The diagram does not attempt to show

interactions between processes, and should not be taken to imply, for example, that information loss and information retention through maturation occur simultaneously (although maturation can affect different tissues differently). Late stage information loss through weathering processes is not shown. ‘Information’, in the context of this figure, refers to primary anatomical, microanatomical and biochemical data, not information regarding the geological processes of fossilization and palaeoenvironment.

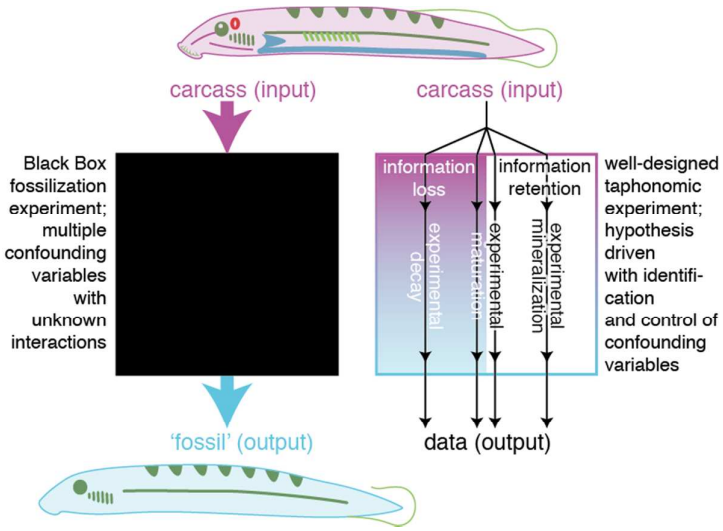

Figure 2. Cartoon illustrating the difference between experiments that attempt to replicate fossilization, treating the process as a black box, and those that focus on the processes of decay, maturation or mineralization. The black box approach reveals little about the processes of information loss and information retention, the cumulative effects and interactions of which ultimately results in a fossil (or, more often, not). Well-designed taphonomic experiments do not attempt to replicate fossilization and do not result in a fossil, but provide reproducible data concerning the processes of fossilization. An ideal taphonomic experiment, with all variables identified and controlled for, is rarely attainable in practice.

REFERENCES

BRIGGS, D. E. G. and KEAR, A. J. 1993a. Decay and preservation of polychaetes: taphonomic thresholds in soft-bodied organisms. *Paleobiology*, **19**, 107-135.

--- 1993b. Fossilization of soft tissue in the laboratory. *Science*, **259**, 1439-1442.

BRIGGS, D. E. G. and MCMAHON, S. 2016. The role of experiments in investigating the taphonomy of exceptional preservation. *Palaeontology*, **59**, 1-11.

BRIGGS, D. E. G. and WILBY, P. R. 1996. Authigenic mineralization of soft-bodied fossils: the calcium carbonate - calcium phosphate switch. *Journal of the Geological Society*, **153**, 665-668.

BUTTERFIELD, N. J. 2002. *Leanchoilia* guts and the interpretation of three-dimensional structures in Burgess Shale-type deposits. *Paleobiology*, **28**, 155-171.

COLLEARY, C., DOLOCAN, A., GARDNER, J., SINGH, S., WUTTKE, M., RABENSTEIN, R., HABERSETZER, J., SCHAAL, S., FESEHA, M., CLEMENS, M., JACOBS, B. F., CURRANO, E. D., JACOBS, L. L., SYLVESTERSEN, R. L., GABBOTT, S. E. and VINTHER, J. 2015. Chemical, experimental, and morphological evidence for diagenetically altered melanin in exceptionally preserved fossils. *Proc Natl Acad Sci U S A*, **112**, 12592-7.

CUNNINGHAM, J. A., THOMAS, C. W., BENGTSON, S., KEARNS, S. L., XIAO, S., MARONE, F., STAMPANONI, M. and DONOGHUE, P. C. 2012a. Distinguishing geology from biology in the Ediacaran Doushantuo biota relaxes constraints on the timing of the origin of bilaterians. *Proc Biol Sci*, **279**, 2369-76.

CUNNINGHAM, J. A., THOMAS, C. W., BENGTSON, S., MARONE, F., STAMPANONI, M., TURNER, F. R., BAILEY, J. V., RAFF, R. A., RAFF, E. C. and DONOGHUE, P. C. 2012b. Experimental taphonomy of giant sulphur bacteria: implications for the interpretation of the embryo-like Ediacaran Doushantuo fossils. *Proc Biol Sci*, **279**, 1857-64.

DONOGHUE, P. C. J. and PURNELL, M. A. 2009. Distinguishing heat from light in debate over controversial fossils. *Bioessays*, **31**, 178-189.

GRIMES, S. T., BROCK, F., RICKARD, D., DAVIES, K. L., EDWARDS, D., BRIGGS, D. E. G. and PARKES, R. J. 2001. Understanding fossilization: experimental pyritization of plants. *Geology*, **29**, 123-126.

GRIMES, S. T., DAVIES, K. L., BUTLER, I. B., BROCK, F., EDWARDS, D., RICKARD, D., BRIGGS, D. E. G. and PARKES, R. J. 2002. Fossil plants from the Eocene London Clay: the use of pyrite textures to determine the mechanism of pyritization. *Journal of the Geological Society*, **159**, 493-501.

GUPTA, N. S., CODY, G. D., TETLIE, O. E., BRIGGS, D. E. G. and SUMMONS, R. E. 2009. Rapid incorporation of lipids into macromolecules during experimental decay of invertebrates: Initiation of geopolymer formation. *Organic Geochemistry*, **40**, 589-594.

GUPTA, N. S., MICHELS, R., BRIGGS, D. E. G., EVERSHED, R. P. and PANCOST, R. D. 2006. The organic preservation of fossil arthropods: an experimental study. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 2777-2783.

HELLAWELL, J. and ORR, P. J. 2012. Deciphering taphonomic processes in the Eocene Green River Formation of Wyoming. *Palaeobiodiversity and Palaeoenvironments*, **92**, 353-365.

KIDWELL, S. M. and BAUMILLER, T. 1990. Experimental disintegration of regular echinoids - roles of temperature, oxygen, and decay thresholds. *Paleobiology*, **16**, 247-271.

MA, X., HOU, X., EDGECOMBE, G. D. and STRAUSFELD, N. J. 2012. Complex brain and optic lobes in an early Cambrian arthropod. *Nature*, **490**, 258-61.

MARTIN, D., BRIGGS, D. E. G. and PARKES, R. J. 2004. Experimental attachment of sediment particles to invertebrate eggs and the preservation of soft-bodied fossils. *Journal of the Geological Society*, **161**, 735-738.

MCCOY, V. E., YOUNG, R. T. and BRIGGS, D. E. G. 2015. Sediment permeability and the preservation of soft-tissues in concretions: An experimental study. *Palaios*, **30**, 608-612.

MCNAMARA, M. E., BRIGGS, D. E., ORR, P. J., FIELD, D. J. and WANG, Z. 2013. Experimental maturation of feathers: implications for reconstructions of fossil feather colour. *Biol Lett*, **9**, 20130184.

MCNAMARA, M. E., ORR, P. J., KEARNS, S. L., ALCALA, L., ANADON, P. and PENALVER MOLLA, E. 2009. Soft-tissue preservation in Miocene frogs from Libros, Spain: insights into the genesis of decay microenvironments. *Palaios*, **24**, 104-117.

MCNAMARA, M. E., VAN DONGEN, B. E., LOCKYER, N. P., BULL, I. D. and ORR, P. J. 2016. Fossilization of melanosomes via sulfurization. *Palaeontology*, **59**, 337-350.

MURDOCK, D., GABBOTT, S. E., MAYER, G. and PURNELL, M. A. 2014. Decay of velvet worms (Onychophora), and bias in the fossil record of lobopodians. *BMC Evol Biol*, **14**, 222.

NAIMARK, E., KALININA, M., SHOKUROV, A., BOEVA, N., MARKOV, A., ZAYTSEVA, L. and GABBOTT, S. 2016. Decaying in different clays: implications for soft-tissue preservation. *Palaeontology*, **59**, 583-595.

PLOTNICK, R. E. 1986. Taphonomy of a modern shrimp: implications for the arthropod fossil record. *Palaios*, **1**, 286-293.

RAFF, E. C., ANDREWS, M. E., TURNER, F. R., TOH, E., NELSON, D. E. and RAFF, R. A. 2013. Contingent interactions among biofilm-forming bacteria determine preservation or decay in the first steps toward fossilization of marine embryos. *Evol Dev*, **15**, 243-56.

RAFF, E. C., SCHOLLAERT, K. L., NELSON, D. E., DONOGHUE, P. C. J., THOMAS, C.-W., TURNER, F. R., STEIN, B. D., DONG, X., BENGTSON, S., HULDTGREN, T., STAMPANONI, M., CHONGYU, Y. and RAFF, R. A. 2008. Embryo fossilization is a biological process mediated by microbial biofilms. *Proceedings of the National Academy of Sciences*, **105**, 19360-19365.

RIEPPEL, O. and KEARNEY, M. 2002. Similarity. *Biological Journal of the Linnean Society*, **75**, 59-82.

SAGEMANN, J., BALE, S. J., BRIGGS, D. E. G. and PARKES, R. J. 1999. Controls on the formation of authigenic minerals in association with decaying organic matter; an experimental approach. *Geochimica et Cosmochimica Acta*, **63**, 1083-1095.

SANSOM, R. S., GABBOTT, S. E. and PURNELL, M. A. 2010. Non-random decay of chordate characters causes bias in fossil interpretation. *Nature*, **463**, 797-800.

SANSOM, R. S., GABBOTT, S. E. and PURNELL, M. A. 2011. Decay of vertebrate characters in hagfish and lamprey (Cyclostomata) and the implications for the vertebrate fossil record. *Proceedings of The Royal Society B-Biological Sciences*, **278**, 1150-1157.

STRAUSFELD, N. J., MA, X. and EDGECOMBE, G. D. 2016. Fossils and the Evolution of the Arthropod Brain. *Curr Biol*, **26**, R989-R1000.